

INHERITANCE OF MUST REACTION AND OTHER CHARACTERS
IN THE PENTAD X AKRONA DURUM WHEAT CROSS

by

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B. S., North Dakota Agricultural College, 1929

A THESIS IS

submitted in partial fulfillment of the

requirements for the degree of

MASTER OF SCIENCE

KANSAS STATE COLLEGE

OF AGRICULTURE AND APPLIED SCIENCE

1931

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DURUM WHEAT BREEDING PROBLEMS

Breeding better durum wheats involves consideration of a number of crop improvement problems. The farmer desires a rust-resistant and productive variety. The grain trade prefers "amber" or white-kernelled to red-kernelled durum wheats and pays accordingly. Roberts (14) has pointed out that the most rust-resistant durum wheats are of low quality for macaroni. The durum wheats as a class are more resistant to stem rust than are common wheats. At Langdon, N. Dak., stem rust is, perhaps, the major limiting factor of production. Since varieties within the durum class vary widely as to their stem-rust reaction, major consideration should be given rust resistance in a breeding program.

Macaroni manufacturers, especially those in the United States, demand a very high quality of semolina. It must be free from grayness or speckiness, and contain a sufficient amount of yellow color. Millers find such semolina can be made best from amber durum wheat of high test weight and protein content and a clear, yellow, translucent color. From the standpoint of the farmer, therefore, it is necessary to breed durum wheat which is satisfactory to the trade. If the farmer cannot obtain the top price for durum together with a higher yield, the wheat will be undesirable and he will grow hard red spring wheat.

Resistance to lodging and shorter stems, resulting in greater ease of handling are other characters to be desired in improved durum varieties. In the durum wheat region, rains and wind often cause serious losses from lodging about the time the wheat starts to ripen. This is especially true in favorable seasons when the growth is heavy. Durum wheat is hard to handle because of its flexible bending stems and long awned spikes. For binding, shocking, and threshing, or for handling with a combine, a durum with shorter and stronger stems, and spikes at a more uniform height is desired. Shorter spikes and awns and possibly smooth awns would be desirable.

Earliness of ripening is not a desirable character if it is accompanied by a reduction in yield. Strains which have a long fruiting period appear the most promising with respect to yield, unless drought intervenes. Frost damage is not likely with reasonably early seeding. Earliness is not essential as related to escape from rust as rust resistance can be bred in new varieties.

Recently bunt has become a serious disease in durums, (7) and (12). Other diseases such as scab, ergot, and leaf rust are present in the durum wheat area, but have not seriously threatened the crop. However, careful observations should be made on the reaction of varieties whenever these diseases occur. Further study may show that resistance to

these diseases and to leaf yellowing may be of sufficient importance to justify breeding for their control.

Yield is the summation of the reaction of the plant characters to environment. It is necessary to breed for yield, inasmuch as yield is due to a complex of inherent characters and physiologic conditions which cannot readily be determined in any other way.

PREVIOUS INVESTIGATIONS

Comparatively few breeding and inheritance studies have been made with durum wheat. More work has been done in crossing durum and vulgare wheats in an attempt to produce common wheats resistant to stem rust. Most of the studies made with durum wheat have also dealt with rust resistance. Harrington and Ammodt (9) reported on the reaction of durum crosses to different forms of stem rust. Hindum x Panted in greenhouse seedling studies gave indications of a single factor difference to rust form 3, and the results with form 1 also were explained by a single main factor difference. No linkage was observed between seed color and rust resistance. These workers obtained a continuous series of strains showing different degrees of resistance and susceptibility, but only six out of 110 F_3 families were highly resistant to both forms of rust. Harrington (8) later reported on the inheritance of resistance to stem rust in the

crosses of Hindum and Kubanka No. 8 with Pentad. Kubanka No. 8 was slightly susceptible and Pentad resistant to rust form 34. Some of the hybrid families were found more susceptible than Kubanka. The results of infecting F_3 and F_4 strains of the Hindum x Pentad cross with form 34 to which Hindum was susceptible and Pentad resistant, indicated the presence of more than one factor. A different reaction was secured for Hindum x Pentad hybrids tested in the greenhouse to form 1 than in the field. In general, according to Harrington, "Reaction to rust was found to be inherited in the same manner as other characters. Several factors were involved and environmental influences modified the expression of rust reaction."

In an attempt to secure a rust-resistant bread wheat by crossing Marquis with Iunillo, a resistant durum, Hayes, Parker, and Kurtzwohl (11) found that they could not recover all the resistance of the durum because it depended on more than one factor and their numbers were not sufficiently large. They reported a ratio of 15 susceptible plants to 1 resistant. The same authors in reporting other durum-common crosses in the same year found rust susceptibility to be dominant. They concluded that the mode of inheritance of rust resistance was the same as that involved in the inheritance of botanical or morphological characters, and that similar technic should be employed in breeding for rust resistance.

Waldron (17) found that progeny from susceptible strains of Kubenska x Power Pipe were intermediate in their rust behavior. He concluded that at least two factors were responsible for rust reaction.

Puttick (15) explained the reaction of the F_2 of a cross between Marquis and Hindum to rust form 19 by a single factor with modifiers, but a single factor did not account for the reaction to rust form 1. However 35 out of 388 F_2 plants were highly resistant to both forms, indicating that there are possibilities in the method of synthetic breeding to obtain varieties resistant to several forms of rust.

Clark and Smith (5) found susceptibility to be dominant to resistance in the durum wheat cross, Rodek x Kahla, with indications of at least two genetic factors being involved.

MATERIALS AND METHODS

The Pentad x Akron cross was studied primarily for the inheritance of rust reaction, because of the importance of the problem and suitability of the parents for such a study. In addition to rust reaction, kernel color, yield, test weight, date of heading, days of ripening, gascoline color value, and crude-protein content of the grain were studied. These characters were studied in relation to the parents and in their relations to each of the other characters.

Pentad, or D-5, is a rust-resistant red durum which was introduced from Russia in 1903 by the North Dakota Agricultural Experiment Station. The variety (2) has nearly white glumes and awns and the kernels are red, short, and plump. The variety was first distributed (4) by the North Dakota Agricultural Experiment Station in 1911, and since that time has been grown extensively in North Dakota. It is considered by the farmers to be particularly desirable for late seeding since it will not be damaged by rust, even though sown late. It is, however, of no value for macaroni because of the grayness and speckiness of its product. On the market it brings a lower price than amber durums, and is largely exported or used for feed.

Akrona is an amber durum which was selected from Akronka, C. I. 1493, in 1912 at the Akron Field Station, Akron, Colo. (3). Results at that station showed Akrona to be the best yielding durum variety. It is early maturing and high in gasoline color value, indicating suitability for macaroni manufacture. Under severe rust conditions, Akrona may be damaged considerably.

Contrasted Characters

The characters studied and the contrasting differences of the two parents under suitable environmental conditions

are:

<u>Characters</u>	<u>Pentad</u>	<u>Akrona</u>
Reaction to stem rust	Resistant	Susceptible
Kernel color	Red	Amber
Yield	Low	High
Toss weight	High	Low
Date of heading	Late	Early
Date of ripening	Late	Early
Gasoline color value	Low	High
Cru-e-protein content	High	Low

The parent varieties, Pentad and Akrona, are well suited for a study of stem rust reaction because Pentad is the most rust-resistant durum wheat known, while Akrona is among the most susceptible. This afforded nearly a maximum range between resistance and susceptibility, where the hybrids might fall in classes not characteristic of either parent.

Although selected primarily for differences as to rust reaction, the parents exhibit rather marked differences in the other characters studied. They are very different in quality. While at the Kansas State Agricultural College in January, 1930, some quality studies of durum wheat varieties were made by the writer. In a comparison of "noodle strips" made from the flour of the two parent varieties, Pentad showed a dull dirty brown color while Akrona had a bright clear yellow color, more intense even than Hindum which is accepted by the trade as the best durum from a macaroni quality standpoint. Pentad is red-kerneled and is

low in gasoline color value, while Akrona has a deep amber kernel color and has a very high gasoline color value.

In case damage from stem rust were very severe, a maximum reduction in yield of Akrona would be expected, while Pented should not be damaged. Test weight should be affected in the same manner. Akrona is one of the earliest of the durum varieties tested, being from one to two days earlier in both heading and ripening than Pented.

The cross between Pented and Akrona was one of several made at the Northern Great Plains Field Station at Mandan, North Dakota, in 1928. The F_1 plants were grown in the greenhouse at Arlington Farm, Virginia, in the winter of 1928 - 1929. Seed from the F_1 plants was sent to Langdon for planting in the spring of 1929. No rust data were obtained on the F_1 plants.

In 1929 the F_2 population was grown in five rows. The kernels were spaced three inches apart in rod rows, one foot apart. One row of each parent was grown on either side of the hybrids. In 1930 the material occupied 168 rows, 150 rows being F_3 strains and the remainder being check rows of the Pented and Akrona parents, which alternated every tenth row. A full rod row with a perfect stand contained 70 plants.

No attempt was made to introduce particular physiologic forms of stem rust. The natural epidemic consisted of the

forms of rust present in the locality. By the use of susceptible varieties in border rows, spacing the seed, and by planting late, a heavy infection was obtained. A study by Dr. M. N. Levine at University Farm, St. Paul, of the physiologic forms present in the locality in 1929 indicated that form 17 was probably responsible for a major part of the infection. Rust collections made in the nursery in 1930 were sent to Dr. Levine, but a report of the identity of the forms present this year is not yet available.

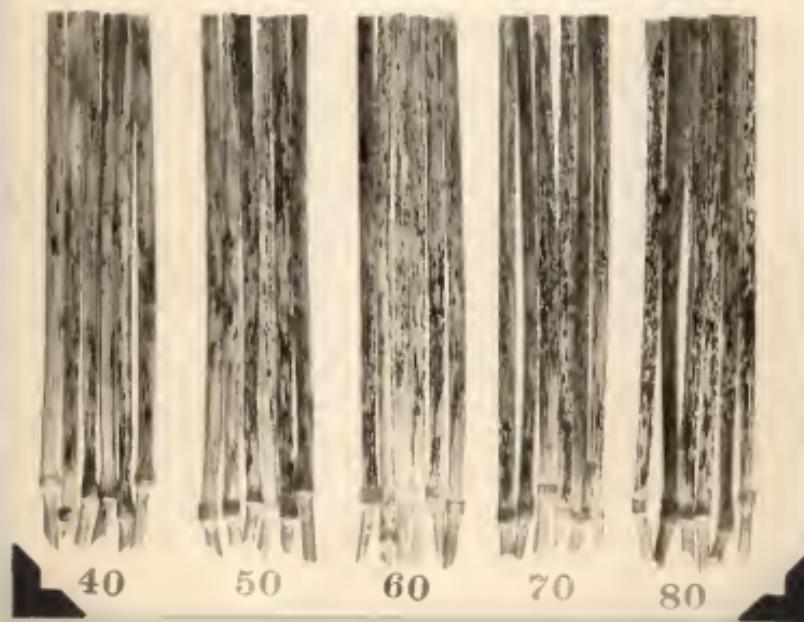
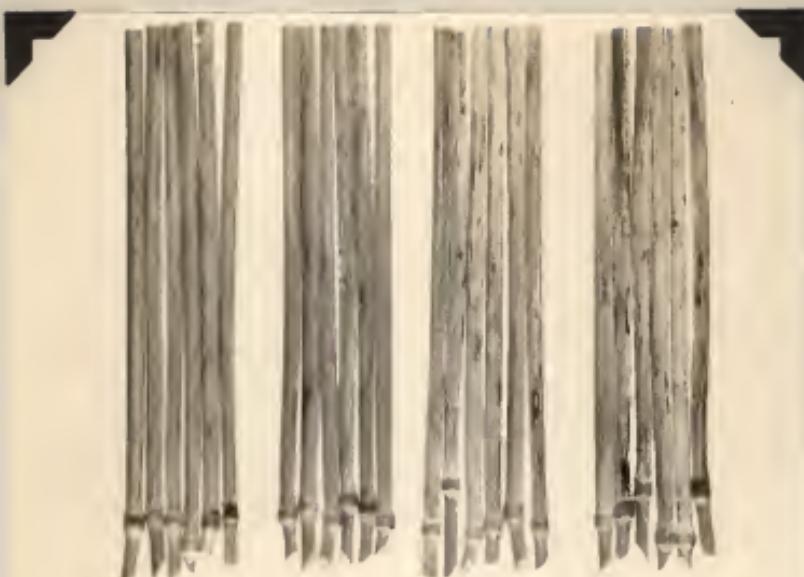
The seasons of both 1929 and 1930 were unusually favorable for developing a severe rust epidemic. In both seasons these durum wheat crosses were planted late and sufficient rain prevented premature ripening. The crop was not too far along when the rust inoculum became abundant, to become heavily infected. Akrona and a ligule-less common wheat were sown in the alleys in 1930 to increase the amount of inoculum present. Of more consequence, however, was the fact that throughout the first week after the first appearance of rust in 1930, the climatic conditions for its development were practically ideal. Very little difference was apparent in the amount of infection in the two years. This is important for comparison of F_2 and F_3 reactions. When the relation of rust to yield is compared for the two years, it is apparent that rust did more damage in 1930 than in 1929.

In both years the plants were pulled when fully ripe

and examined individually for rust infection. The rust reaction was quantitative in appearance, there being no distinct categories. Each plant, therefore, was classified for amount of stem rust in the following classes: trace, or two per cent, and in ten per cent frequency classes 10, 20, 30, 40, 50, 60, 70, and 80, according to its infection. These degrees of infection are shown in Plate 1. The percentages were considered the center of their class, i. e., 10 per cent was the midpoint of 5 to 14 per cent, and 80 the midpoint of 15 to 24 per cent, etc.

In the F_2 generation each plant was threshed separately and the individual plant yields recorded. In 1930, after the rust classification was completed, the plants of each strain or row were put together and threshed as an F_3 bulk. The average yield per plant was calculated by dividing the yield per row by the number of plants. On the bulk grain from the F_3 strains and parent checks, test weight, gasoline color value, and crude protein content were determined.

Plate I.-Stem rust infection classes used in the classification of the F_2 and F_3 generations of the Pentad x Alkrona durum wheat cross at Langdon, N. Dak., in 1929 and 1930.



SEGREGATION OF CHARACTERS

The results for each of the characters studied follow in the order listed above. Major consideration is given to stem-rust reaction.

Stem-Rust Reaction

A careful separation of the parent and F_2 plants was made in 1929 into the percentage classes for stem-rust infection. The results from the progenies of five F_1 plants, including reciprocal crosses, were compared, and as there were no apparent differences among the F_2 families, they were combined.

The percentage rust classes of the parents and F_2 hybrid plants of the Pentad x Akrona durum wheat cross are shown in Table I and Fig. I. A population of 184 F_2 plants was grown. Their distribution, in relation to that of the parents, indicates an intermediate inheritance or that susceptibility may be partially dominant. Thirty-four and six tenths per cent of the F_2 hybrid plants were in the classes of 40, 50, and 60 per cent. This rust reaction is similar to that of Akrona, the susceptible parent. Only 5.4 per cent of the hybrid plants were in the 10 per cent class, which included 39.8 per cent of the plants of Pentad, the resistant parent. There were no hybrid plants in the trace

Table I.—Distribution of parent and F_2 hybrid plants of the Pentad \times Acrea durum wheat cross into stem rust percentage classes at Langdon, N. Dak., in 1929

		Number of plants by percentage classes						Average stem rust infection per cent	
		0	10	20	30	40	50	Total	
Parent								89	0.2
Parents and cross		55	66						
Numbers									
Percentage		60.2	39.8					100	
F_2 hybrids									
Numbers		10	36	75	45	16	5	194	31.7
Percentage		5.4	18.9	41.1	24.4	8.3	1.6	100	
Acrea									
Numbers		7	69	15	91	80.9			
Percentage		7.7	75.0	16.5	100				

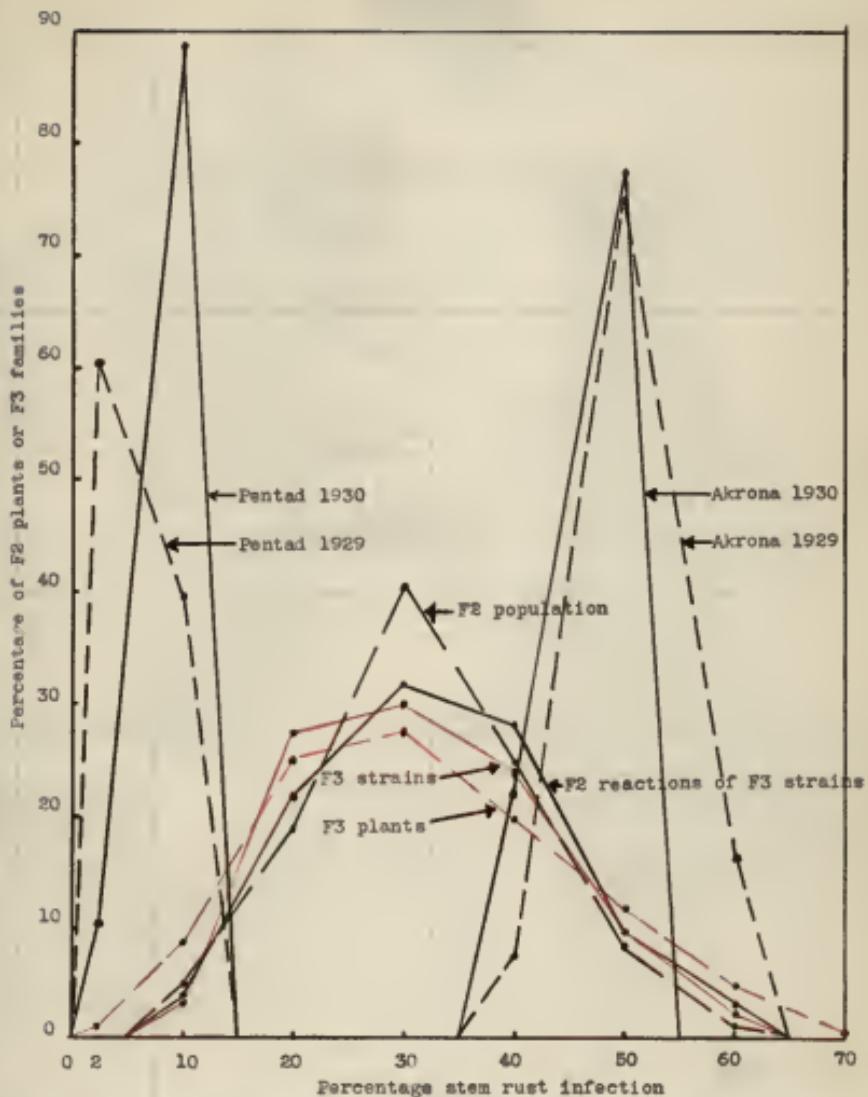


Figure 1. Stem rust distribution for parents, F2 population, and reaction in F2 and F3 of 150 F3 strains of the Pentad x Akrona durum wheat cross at Langdon, North Dakota, in 1929 and 1930

or two per cent class, while 60.2 per cent of the Pentad plants were in this class. Thus there was a definite tendency towards susceptibility, with only 10 F_2 plants showing resistance within the range of Pentad, while 64 F_2 plants were fully as susceptible as Akrona. The average rust percentage, 31.7 per cent, for the F_2 hybrids approaches 50.9 per cent, the average of Akrona, more closely than 5.2 per cent, the average of Pentad. The numbers of resistant, intermediate, and susceptible plants do not give a close fit to a single genetic factor ratio.

Only 150 of the 184 F_2 plants were selected for further study and these were not a true random sample in that they contained a smaller proportion of strains from the 30 per cent modal class, and a larger proportion of the other classes. The stem-rust infection of the selected F_3 strains shows a similar reaction or symmetry of curve to the F_2 population, as shown in Fig. 1. In comparing the curves showing the average infection of the F_3 strains with their infection in F_2 , a slight shift toward resistance is indicated. This is as might be expected. If susceptibility is dominant or partially dominant, the breaking up of heterozygous susceptible strains will tend to increase the proportion of resistant plants. The difference in the means for stem-rust infection of the F_2 plants and F_3 strains, 32.2 and 31.6 per cent respectively, is not statistically significant.

It is impossible to say definitely whether or not the F_2 rust reaction was similar to the F_3 reaction because of the possibility of error introduced by the difference in the nature of the epidemics in the two seasons. Judging from the parental rust reactions in the two years, the two epidemics caused about the same amount of infection, for although Pentad showed 1.2 per cent less rust in 1930, Akrona showed 2.2 per cent more than in 1929. Pentad showed strong resistance and Akrona high susceptibility in both seasons.

A comparison of the curve of the F_3 based on a total of 8,337 plants in comparison with that of the F_2 for 185 plants reveals a similar type of distribution. In F_3 , the intermediate classes, which may be assumed to contain a larger proportion of segregating strains, show a decrease in the percentage of the total, while the extreme resistant and susceptible classes, supposedly more homozygous, show an increase in the percentages. Some F_3 plants were observed in the extreme classes of 2 and 70 per cent. Thus it was possible to recover F_3 plants having the strong resistance to stem rust of Pentad. The presence of a few F_3 plants in the very susceptible 70 per cent class suggests transgressive segregation.

The average infection of the F_3 strains, distributed in five per cent frequency classes and arranged according to the F_2 percentage classes, is summarized in Table II.

The average distribution of the F_3 strains shows that of 8 plants classified as having 10 per cent rust in F_2 , only two or 25 per cent were as resistant as Pentad. One was susceptible and evidently escaped infection in 1929. The corrected F_2 percentage shows only 1.6 per cent of the total F_2 to be resistant. At the other end of the corrected distribution there were 16.2 per cent of the F_2 plants as susceptible as Akron. The fact that the resistance of Pentad was difficult to recover indicates the presence of several genetic factors. If the susceptible segregates found in the 70 per cent class were caused by the usual type of transgressive segregation, some very resistant segregates would also be expected. The fact that these were not obtained in this cross suggests the presence of inhibiting or modifying factors.

Table II.—Average stem-ear infestation of 120 F₁ strains of the Portola X Aurora durum wheat cross in comparison with the parents and frequency classes, at Langdon, N. Dak., in 1950 and 1959.

1950 average infect- ion	Per- cented	1950 percentage classes and P_2 starting group										Ave- rage	Corrected P_2	
		No.	%	No.	%	No.	%	No.	%	No.	%			
5	7													
10	2	1	25.0											
15	1	12.3	3	15.2	4	6.5							7.0	
20	5	37.5	11	35.5	6	12.5	2	4.7					14.6	
25	1	12.3	9	27.5	10	30.0	4	9.3	1	6.7			17.2	
30				6	10.2	10	37.5	3	11.6	2	15.3			22.3
35				1	3.0	6	12.5	0	16.0	1	6.7			10.6
40				1	3.0	3	6.5	10	25.0	2	15.8			10.0
45				1	2.1	6	16.0	4	26.7	1	35.3			7.1
50	1	12.3												
Total		6	100.0	25	100.0	35	100.0	45	100.0	55	100.0			10.2
Average		21.2	25.5	26.0	30.5	45.5	45.5	55.0	55.0	60.0	60.0			10.0
Original P_2		6.4	16.0	41.1	24.4	6.6	6.6	1.0	1.0	1.0	1.0			100.0

The high correlation between the F_2 and F_3 results indicates that the same physiologic form or group of forms of stem rust were present in the two seasons, and that a high degree of accuracy was attained in the classification of the F_2 plants. The 8 plants which were classified as having 10 per cent of rust in F_2 produced F_3 progenies that averaged 21.2 per cent rust. Thirty-three F_3 strains from F_2 plants with 20 per cent rust averaged 23.5 per cent rust. Forty-eight F_3 strains from F_2 plants having 30 per cent rust averaged 28 per cent rust. The 43 F_3 strains from F_2 plants having 40 per cent rust averaged 38.5 per cent rust. Fifteen F_3 strains from F_2 plants having 50 per cent rust averaged 43.5 per cent rust. Three F_3 strains from F_2 plants having 60 per cent rust averaged 50 per cent rust. The epidemics in the two seasons were similar as to amount of infection. The principal exception observed is that one plant showing 10 per cent rust produced an F_3 progeny with an average of 50 per cent rust. This may have been caused by scab and premature ripening of the F_2 plant preventing normal infection of rust.

Standard deviation. The standard deviation of rust infection was determined for each F_3 strain and parent check row, in order to show the variability of the hybrids in comparison with the parents.

The relation between the average stem-rust infection and the standard deviation for rust infection of the parent check rows and the 150 F_3 strains is shown in Table III. Most of the hybrids are much more variable than the Pentad parent, and many of them are more variable than Akrona. The two hybrid strains having an average infection within the limits of the resistant Pentad parent, are more variable than Pentad. This indicates that they did not breed true for resistance. The data as a whole indicate that the relation between rust infection and its variability is not linear. The classes intermediate for rust reaction tend to have a higher standard deviation than the more resistant or more susceptible strains. This indicates that the intermediate rust classes include a larger proportion of heterozygous strains.

The Akrona check rows have a higher standard deviation than the Pentad check rows. Akrona can scarcely be considered any less homozygous than Pentad, since both are pure lines. If a variety had an immune reaction, its standard deviation would be zero. Hence it may be that with the increasing amounts of infection, an increasing value should be taken as the maximum standard deviation consistent with homozygosity. With this in mind, a line was drawn in Table III. laying off the maximum standard deviation of the parents. On this basis, 33 out of 150 strains may be assumed to be

Table III.—Average stem-rust infection and standard deviation of parent check rows and of 150 $\frac{1}{2}$ strains of the Pentad x Aurora durum wheat cross, into frequency classes, grown at Langdon, N. Dak., in 1930

Per cent stem rust	Standard deviation							Total	Ave. rust
	2.5	3.5	4.5	5.5	6.5	7.5	8.5		
Pentad	1	0	0	0	0	0	0	7	0.41
10	1	0	0	0	0	0	0	4	0.41
Total	1	0	0	0	0	0	0	9	0.41
Hybrids	1	0	0	0	0	0	0	1	0.41
5	1	0	0	0	0	0	0	2	0.41
10	1	0	0	0	0	0	0	2	0.41
15	1	0	0	0	0	0	0	2	0.41
20	1	0	0	0	0	0	0	2	0.41
25	1	0	0	0	0	0	0	2	0.41
30	1	0	0	0	0	0	0	2	0.41
35	1	0	0	0	0	0	0	2	0.41
40	1	0	0	0	0	0	0	2	0.41
45	1	0	0	0	0	0	0	2	0.41
50	1	0	0	0	0	0	0	2	0.41
55	1	0	0	0	0	0	0	2	0.41
Total	9	14	49	43	23	11	2	1	160
Aurora	1	2	1	1	1	1	1	1	4
45	1	2	1	1	1	1	1	1	4
50	1	2	1	1	1	1	1	1	4
55	1	2	1	1	1	1	1	1	4
Total	3	6	14	13	7	4	3	3	40.00

homozygous for their rust reaction. This includes 22 per cent of the strains, and leaves 78 per cent which are apparently still heterozygous after the second segregating generation.

According to Jones' table in Hayes and Garber (10) showing the amount of heterozygosity in a hybrid population in succeeding generations when varying numbers of factors are concerned, very nearly 78 per cent heterozygous individuals may be expected in the second segregating generation when five genetic factors are concerned. On this basis five genetic factors may be responsible for the stem-rust reactions observed in this cross. To prove this, it would be necessary to test further the homozygosity of the strains by their reaction in the F_4 and later generations. This arbitrary method of determining the homozygous strains may be subject to criticism, but at the present stage of the investigation appears to be the best method available. This hypothesis assumes equal effects of all the genetic factors concerned. Actually, it is possible that two or three major factors and other minor factors are responsible for the rust reactions observed. Some of the factors may control morphologic and others physiologic differences related to rust reaction. It will be noted that none of the strains had as low standard deviations as did the Pentad parent check rows. This indicates that 150 strains were not enough to recover, in a homozygous condition, the rust resistance of Pentad.

Kernel Color

Kernel color is of considerable importance in a durum wheat breeding program. The data for kernel color are in distinct categories, whereas the data on rust reaction and the other characters are in frequency classes.

Pentad, the rust-resistant parent, has a dark red kernel color and has the least desirable quality of the commercial durum varieties. Akrona, the rust susceptible parent, has kernels lacking the red pigment. Although not commercially grown, experimental tests have indicated that Akrona should be highly satisfactory from a quality standpoint. Thus in the parents used in this cross there is a very definite difference and value in color of kernel.

The segregation for kernel color in the F_2 generation for the Pentad x Akrona durum wheat cross is shown in Table IV. In F_2 too many amber kerneled plants were obtained to give a satisfactory fit to a 3:1 ratio. The observed numbers give a fair fit to a 9:7 ratio, the odds against the occurrence of such a deviation due to chance being 7 to 1. The segregation for kernel color in the F_3 generation is shown in Table V. The results do not show a very good fit to the 1:8:7 ratio, $P = 0.02$, although it is much better than to a 1:2:1 ratio.

Table IV-Segregation for kernel color and goodness of fit to 3:1 and 9:7 ratios for the
 F_2 generation of the Pentad x Akren durum wheat cross grown at Langdon, N.Dak.,
in 1959 and 1960

	Kernel color			Dev.	P.E.	D/P.E.	Odds
	Red	Amber	Total				
Observed	114	70	184				
Calc. 3:1	128	46	174	16	3.96	4.0	142:1
Calc. 9:7	103.5	80.5	184.0	10.5	4.54	2.3	7:1

Table 7. Segregation for kernel color in F_2 and goodness of fit of corrected F_2 to 1:1:1 ratio in the Pentad \times Acreum durum wheat cross grown at Langdon, N. Dak., in 1939 and 1950

F_2 kernel color and breeding behavior.	F_2 Segregation		Original F_2		Corrected F_2	
	Numbers	Per cent	Numbers	Per cent	Percent	Numbers Obs. - Calc.
Red			114	62.0	11.1	20.6 11.5
Breeding true	15	17.9			50.0	95.5 95.0
Segregating	69	82.1				
Total	94	100.0	70	38.0	38.0	70.0 30.6
Amber						
Breeding true	66	100.0				
Total	160		134	100.0	100.0	184.0 184.0

$$\chi^2 = 0.414 \quad P = 0.02 \quad \text{Odds} = 49:1$$

The 9:7 or 1:8:7 ratio could be explained on the basis of two complementary factors for red. Thus Pentad would be AAbb and Akrona sabb. The F_1 , AaBb would be red. In the F_2 , all plants carrying at least one dominant allelomorph of each factor pair would be red, while the remaining plants would be amber, thus giving nine red plants to seven amber plants. In the F_3 the ratio would be one homozygous red and eight segregating to seven amber. Thus one AAbb would breed true for red; two AABb and two AaBB would segregate 3:1 red to amber, and four AaBb would segregate 9:7 red to amber; and the remaining combinations would have amber kernels.

The F_3 population was not a random sample for kernel color, since a larger proportion of the amber than of red-kernelled plants were selected for growing in F_3 because of the probably greater practical value of the amber types. The strains which bred true for amber color showed indications of different degrees of color from light to gray amber. Of the 84 red-kernelled plants grown, 15 bred true for red. This is a fairly good fit to the expected ratio of 1:8, homozygous red to segregating, $D/E = 2.9$. However, when the observed numbers in the F_3 are used to calculate the F_2 for a random sample, the fit to a 1:8:7 ratio is not good, due to a shortage of amber strains and a surplus of red. The value of $P_{<0.02}$, indicates that only once in about 49 trials

would as great a deviation be expected due to chance alone.

While other crosses with Pentad (9) have indicated a single factor difference for kernel color, the results from the present cross give a much better fit to the 1:8:7 ratio than to a 1:8:1 ratio which would be expected in F_2 if the kernel color were due to a single factor difference. It is possible that the color of Akrona is caused by different factors than that of other amber durum varieties. If two complementary factors are responsible for the kernel color differences observed in this cross, it should be possible to prove it by crossing two amber kornelized strains and securing a red-kornelized strain. Thus if AAbb was crossed with aaBB, both amber strains, the F_1 would appear red, AaBb, and would segregate in subsequent generations in the same manner as a cross between AAbb and aaBB.

Yield per Plant

Yields were obtained in 1929 on an individual plant basis. The average yield of 88 plants of Pentad was 5.51 grams per plant and the average yield of 91 plants of Akrona was significantly higher, 6.68 grams per plant. The average yield of 184 F_2 hybrid plants was intermediate between the parents, 5.79 grams. The yields for 1930 were the average plant yield for the strains and parental check rows. The average yields per plant for the parents and 150 F_2

strains are given in Table VI. In both the F_2 and F_3 generations the average yields of the hybrids are intermediate between the yields of the parents. However, the order of the yields of the parents in the two years was reversed. In 1930 Pentad yielded on the average 4.34 grams and Akrona only 2.62 grams per plant. This apparent inconsistency is largely accounted for in the difference in damage caused by rust in the two years. As has been mentioned, conditions for rust were ideal immediately after its appearance in 1930, and although the amounts of infection were very similar in the two years, the rust in 1930 became so well established that it did much more damage. That Pentad yielded less in 1930 than in 1929 may be attributed to the fact that moisture conditions in the later stages of growth were more favorable in 1929 than in 1930.

Table VI-Yields per plant of parents and 150 F_2 strains of the Pentad \times Akron durum wheat cross, grown at Langdon, N. Dak., in 1930

Parents and cross	Yield per plant, gns.							Total no. of rows	Mean and probable error
	1.0	2.0	3.0	3.0	4.0	4.5	5.0		
Pentad	1	1	3	0	3	1	9	4.54±0.10	
F_2 strains	7	10	18	45	44	30	8	1	150
Akron	1	1	2	2				9	2.68±0.15

In both the F_2 and F_3 , the yields of the hybrids were slightly nearer the yield of Pentad than that of Akrona. This may be interpreted to indicate that rust does proportionately less damage in the lesser infected plants than in those more heavily infected. That is, increasing the rust infection from 10 to 20 per cent would not cause as great a reduction in the yield as an increase from 40 to 50 per cent. This is in line with what frequently is observed in the field, namely, that wheat may show little damage from 10 to 20 per cent of rust, while 40 to 50 per cent infection may cause a sharp reduction in yield and test weight.

Test Weight Per Bushel

It was impossible to secure test weights for the F_2 generation since only a few grams were produced from each plant. In the F_3 generation, test weights were taken on all strains producing sufficient seed to measure in a half pound test kettle. Only 72 of the 150 strains produced sufficient seed to give test weight readings. The lack of sufficient seed for test weight was due either to damage to the yield from rust or to lack of sufficient plants to produce the necessary yield per row. The most important phases of test weight are brought out later in the discussion of its relations with other characters. The frequency distribution for the test weight of the hybrids on which test weights were obtained is shown in Table VII.

Table VII.—Frequency distribution and means for test weight per bushel on 72 of the
 160 F_3 strains of Pentad x Alcorn and on the parents at Langdon, N. Dak.,^a
 in 1930

Pounds	Test weight per bushel, lbs.						Mean and probable error
	65	66	67	68	69	70	
Pentad			1	7		0	69.1±0.01
F_3 strains	1	4	10	24	9	72	65.5±.09
Alcorn		1				1	66.0

The results show that the mean of the hybrids is intermediate between the parents for test weight. Nine hybrid strains had test weights heavier than any of the Pentad check rows. Many of the strains not tested probably had test weights lower than the one Akrona check row from which it was possible to obtain a test.

Date of Heading

In 1930 the date of heading was recorded on each F_3 strain as an entire row. No attempt was made to take the notes on a plant basis. No heading data are available on the F_2 . The distribution and means of the heading dates on the 150 F_3 strains of Pentad x Akrona cross and parents are shown in Table VIII.

Table VIII.-Distribution and means of heading dates on 150 P_3 strains of Pentad x Akrons and the parents at Langdon, N. Dak., in 1950

Parents and cross	Heading date - July						Mean and probable error
	14	15	16	17	18	19	
Pentad		2	6	1			9 16.9±0.58
P_3 strains	2	64	47	23	4	7	1 160 16.9± .06
Akrons	6	8	1				9 15.4± .46

Although the difference between the parents is only one and one-half days and is hardly significant in view of their probable errors, Akron repeatedly has been observed to be from one to three days earlier in heading than Pentad. The mean heading date for the 150 F_3 strains is intermediate between that for the parents. However, eight strains were later and two strains were earlier than either of the parents, possibly indicating transgressive segregation. This may be important from a plant breeding standpoint if it is found that the earlier heading varieties are superior for yield or quality.

Date of Ripening

Dates of ripening were taken on the F_3 strains on a row basis. The distribution and means of the ripening dates on 150 F_3 strains of Pentad x Akron cross and parents grown in 1930 are given in Table IX. The results are somewhat similar to the data obtained for heading dates. Akron was two days earlier than Pentad. The F_3 strains averaged one day earlier than Pentad and one day later than Akron. There was indication of transgressive segregation for earliness. It appears desirable to test these transgressive segregates in the F_4 and later generations to determine more accurately their comparative earliness and whether or not they are homozygous for earliness.

Table IX.-Distribution and means of ripening dates on 160 F_3 strains of Pentad x Arvensis
and the parents at Langdon, N. Dak., in 1950

Parents and cross	Ripening date - August					Mean and probable error
	18	19	20	21	22	
Pentad			7	2	0	21.4±0.19
F_3 strains	7	29	39	52	12	30.4± .07
Arvensis	6	4			0	19.4± .114

Gasoline Color Value

The gasoline color values were determined by the standard A. O. A. C. method with such minor alterations as seemed desirable. According to Schertz (15), the use of a spectrophotometer is much more accurate than the colorimeter in the reading of the color value. However a spectrophotometer was not available, and since the colorimeter gave consistent and significant differences in the carotin content of the parents, it was considered satisfactory for the purpose desired. As was found by Ferrari and Bailey (6), difficulty was experienced in the present study in filtering where the sample was shaken immediately before filtering and also the use of several thicknesses of filter paper, although clarifying the solution causes more carotin to adsorb to the paper. Consequently, after standing for some time, the solution was decanted and filtered through a single filter paper. Thus no difficulty was experienced in obtaining a clear solution. However, there were indications of adsorption of carotin by the filter paper, or by small flour particles on the filter where the filtering was not carefully manipulated. The readings were made on 5 gram samples of the ground whole wheat from each row or strain. It was found that grinding to a uniform fineness was very necessary for securing comparable results.

Gasoline color values are determined on durum wheats in an attempt to distinguish those of poor quality from those of good quality for the manufacture of semolina. Bailey(1) expresses doubt that the content of carotinoid pigment is the sole factor in determining the visual appearance of macaroni. He suggests that the physical structure of the semolina particles may also affect the appearance of the macaroni in much the same way as the appearance of the endosperm of the wheat berry is determined in a large part by its relative density. This point is important and must be considered before final judgment can be rendered on the quality of any particular durum wheat. However, the amount of carotinoid pigment is believed to be one of the most important factors in durum wheat quality and furthermore it is readily measured, and on small samples, whereas the physical structure of the endosperm, the amount of grayness, and the nature of the protein are rather abstract qualities, more difficult to evaluate. Therefore, the determination of the carotinoid pigment is considered important, particularly in a study of hybrid material.

Theoretically, a durum wheat with high carotin content, as indicated by high gasoline color value, is more desirable than one of low carotin content and giving a low gasoline color reading. Actually, some of the durum varieties of moderate carotin content are very desirable and may be even

Table I.-Frequency distribution and means for gasoline color values of the parents and 150 F_2 strains of the Pentad x Alkoma durum wheat cross grown at Langdon, N. Dak., in 1950

Percentile and crosses	Gasoline color values						Mean and probable error
	0.6	0.8	1.2	1.8	1.8	2.1	
Pentad	5	6					0.75±0.05
F_2 strains	1	45	69	29	16	6	1.25± .01
Alkoma				4	5	9	1.97± .03

Crude Protein Content

Crude protein determinations were made on the parents in 1929 and on the parents and F_3 hybrids in 1930.

In 1929 the parents showed but little difference in protein content, both of them being high. Pentad had an average of 15.2 per cent protein and Akrona had 15.1 per cent. The frequency distribution and means for crude protein content of the parents and 149 F_3 strains in 1930 are given in Table XI. Pentad again was high with an average of 14.9 ± 0.08 per cent protein. As will be pointed out in a discussion of the correlations, the low average protein content of Akrona in 1930, 13.5 ± 0.08 per cent, is very likely a result of the damage from rust.

The average protein content of the F_3 hybrids, 14.1 ± 0.04 per cent was intermediate between the parents. Three F_3 strains were lower in protein content than any of the Akrona rows. There was some tendency for low protein strains to predominate. This may reflect the tendency toward susceptibility to rust rather than indicate a partial genetic dominance of low protein content.

¹⁴ The crude protein determinations were made in the Research Laboratory of the Bureau of Agricultural Economics, Washington, D. C.

Table XI.—Frequency distribution and means for crude protein content of the parents and 169 F_3 strains of the *Pentad* x *Akron* durum wheat cross grown at Langdon, N. Dak.,
in 1950

Parents and strains	Per cent crude protein *					Mean and probable error			
	12.5	13.0	13.5	14.0	14.5				
<i>Pentad</i>	5	4	3	0	0	14.9±0.08			
F_3 strains	5	12	13	53	20	15	0	14.9	14.1±0.04
<i>Akron</i>	2	0	0	1			0	13.0±0.08	

* Reduced to 15.0% moisture basis.

more desirable commercially than one with an extremely high gasoline color value. Perhaps the use of the gasoline color test in studying the quality of strains of durum crosses will be most valuable when used primarily to make certain that the new strain has sufficient yellow color to make it commercially desirable.

Gasoline color values were determined on the parent check rows in 1929, and on the individual F_3 strains of the Pentad x Akrona cross and on the parents in 1930. In 1929 Pentad had a gasoline color value of 0.71, and Akrona 1.43. The frequency distribution and means for the data obtained on F_3 strains and parents in 1930 are shown in Table X. Akrona had a very much higher color value than Pentad, their mean color values being $1.97 \pm .03$ and $0.78 \pm .03$, respectively. The color values of the F_3 strains indicated a tendency for low color value to be partially dominant. The mean value of the F_3 strains was $1.25 \pm .01$, which is nearer the mean of Pentad than of Akrona. Forty-four out of 150 F_3 strains or 29.3 per cent were within the range of the Pentad or low color parent, while only 10, or 6.7 per cent were within the range of the Akrona, or high color parent. These observations are in line with observations made on strains of Pentad x Mindum, where considerable difficulty was experienced in finding strains carrying the desirable color of the Mindum parent.

ASSOCIATION OF CHARACTERS

In order to conduct wheat breeding effectively it is necessary to understand the inter-relations of the several characters under observation. For instance if it is known which characters have the major effect on yield and quality and their inter-relation, it is possible to select for the desired type more intelligently and with greater chances of success.

Characters Correlated

Simple correlation coefficients are shown in Table XII for pairs of the quantitative characters studied in the Pentad x Akron cross. While none of these values is high they are all important in showing either no relation between characters or a significant tendency for the characters to be related.

Table XIII.—Simple correlation coefficients for pairs of characters in the Pentad x Akron durum wheat cross grown in 1929 and 1930, at Langdon, N. Dak.

Characters correlated	Number of variates	r	P.E.	r/P.E.
Stem rust infection in F_3 and:				
F_2 rust	150	+ .673± .030		22.4
Yield per plant	150	- .311± .050		6.2
Test weight	72	- .436± .064		6.8
Heading date	150	+ .130± .054		2.4
Ripening date	150	- .010± .055		.2
Gasoline color value	150	+ .067± .055		1.2
Protein content	149	- .364± .048		7.6
Yield per plant in F_3 and:				
F_2 yield	150	+ .002± .056		.04
Test weight	72	+ .229± .075		3.1
Heading date	150	- .221± .052		4.2
Ripening date	150	+ .230± .052		4.4
Gasoline color value	150	+ .047± .055		.9
Protein content	149	+ .011± .052		.2
Test weight of F_3 strains and:				
Heading date	72	- .396± .067		5.9
Ripening date	72	+ .229± .075		3.1
Gasoline color value	72	- .568± .055		10.1
Protein content	71	+ .026± .080		3.3
Heading date of F_3 strains and:				
Ripening date	150	+ .320± .049		6.5
Gasoline color value	150	- .040± .065		.7
Protein content	149	+ .258± .062		4.6
Ripening date of F_3 strains and:				
Gasoline color value	150	- .266± .051		5.2
Protein content	149	- .247± .052		4.7
Gasoline color of F_3 strains and:				
Protein content	149	- .156± .054		2.9

Simple correlations. The correlation between the average stem-rust infection on the 150 F_3 strains and the infection recorded on the F_2 plants from which these strains were derived, was $+0.673 \pm 0.030$. This is both important and significant. The distribution of the data is shown in Table 2.

The correlation between stem-rust infection and yield of F_3 strains, -0.311 ± 0.050 , is significant and may be considered of some importance from a plant breeding standpoint. It shows a definite tendency for the strains which are more susceptible to rust to be lower in yield. This value shows how the yield was reduced by rust in 1930, when conditions were so favorable for rust development.

Yield apparently is governed by a more complex series of factors than test weight. Test weight appears a better indication of damage caused by rust than yield as the correlation coefficient between rust infection and test weight, -0.436 ± 0.064 , is more important. Because of lack of sufficient seed, test weight was obtained on only 72 of the 150 F_3 strains. The effect of rust on test weight probably would have been more clearly shown had it been possible to get test weights on every strain, because lack of sufficient seed was principally due to damage from rust. This is proven by a comparison of the average rust percentage of rows on which test weights were obtained, and that of the

rows on which test weights were not obtained. The average rust on rows that produced enough grain to determine test weights was 29.4 per cent as compared with an average rust infection of 35.6 per cent for the rows that did not produce enough grain to determine test weight.

The effect of rust on protein is shown by the negative correlation, -0.364 ± 0.048 . Thus the strains more susceptible to rust tended to be lower in protein. This is in line with the reaction of the parents. In 1930, when damage from rust was severe, Akron, the susceptible parent, was significantly lower in protein than Pentad, the resistant parent. This relation between protein content and rust infection may appear contradictory to the generally accepted ideas; i. e., rust causes shrivelling and shrivelled grain is higher in protein. However, Shollenberger and Kyle(16) conducted studies on the relation of protein to test weight and found that the relation between them was curvilinear. In 1290 samples from the spring wheat states in the years 1915 to 1923 they found that for samples weighing more than 53 pounds per bushel, the correlation between test weight and protein was negative, while for samples weighing less than 53 pounds per bushel, the correlation was positive. They observed that test weights below 53 pounds occurred rarely except under conditions of severe rust, and concluded that rust was responsible for the lowering of protein in

those cases. The lowering of test weights to about the 53 pound level was attributed to lack of moisture which arrests the growth and shortens the fruiting period. It would appear in the Pentad x Akron cross that rust rather than moisture was the limiting factor, and hence the negative correlation between rust and protein agrees with the results cited.

The correlation between yield and test weight, +0.229±.075 is positive but not important and barely significant. It shows a slight tendency for strains producing a high yield to be high in test weight. This correlation, however, does not give the full relation between yield and test weight, since only 72 of the 150 strains produced enough seed for test weights to be determined. The strains on which test weights were taken yielded on the average 4.08 grams per plant, while the strains on which test weights could not be obtained averaged only 3.25 grams per plant. Not all of this difference can be attributed to rust, however, since there was some difference in the number of plants per row, due to the death of varying numbers of plants, during the season. The average number of plants per row in the strains on which test weight could not be determined was 52.8, while the average for those strains having test weight readings was 58.1 plants. Because of the rust damage and the negative correlations of rust with test weight and yield, it

would follow that the positive correlation between yield and test weight should have been larger.

A small negative correlation between yield and date of heading, $-0.221 \pm .052$ is statistically significant but not important. It indicates a slight tendency for the early heading strains to yield more than those which headed later.

The correlation between yield and date of ripening is positive, $+0.230 \pm .052$, and is also statistically significant but not important. This indicates that a long fruiting period is desirable and tends to increase yield.

A fairly important negative correlation, $-0.396 \pm .067$, was found between test weight and date of heading. A less important positive correlation, $+0.229 \pm .075$ was found between test weight and ripening. This shows the tendency for earlier heading and later ripening strains to be the higher in test weight, and again emphasizes the desirability of a long fruiting period. An important negative correlation, $-.558 \pm .055$, was found between test weight and gasoline color value. This indicates that strains with higher test weight may be expected to have a lower gasoline color value. The positive correlation, $+0.320 \pm .049$, between dates of heading and ripening is important and shows a significant tendency for those strains which were early in heading to be early in ripening. The positive correlation of $+0.238 \pm .052$ between heading date and protein content indicates

that the later heading strains have a slight tendency to be the higher in per cent crude protein. The negative correlation, -0.266 ± 0.051 , between date of ripening and gasoline color value is statistically significant but not important. This indicates that the later ripening strains have a slight tendency to have a lower gasoline color value. The small negative correlation of -0.247 ± 0.052 for date of ripening with protein content shows a small but significant tendency for the later ripening strains to be the lower in protein.

Partial correlations. Partial and multiple correlation coefficients for certain of the characters studied are given in Table XIII. The characters on which partial correlation coefficients were calculated were selected on the basis of their probable causal relations with the other characters. Thus, of the characters studied in the cross, yield, test weight, gasoline color value and per cent of crude protein were considered to be the resulting characters. The characters affecting these were selected from a study of the relations indicated by the simple coefficients of correlation. Stem-rust infection, dates of heading, and ripening were considered to be the characters affecting yield, test weight, and crude protein content. Test weight and date of ripening appeared to be the characters affecting gasoline color value. It appeared that a better picture of the true relations between the resulting and an affecting character might be obtained if the other affecting characters could be held constant.

Table XIII.—Simple, partial, and multiple correlation coefficients between certain characters in the Penta x Akron durum wheat cross grown in 1939 and 1940 at Langdon, N.Dak.

Characters correlated	Subscript number	Simple correlation	Partial correlation	Multiple correlation
Yield and F_5 rust	1	$r_{71} = -0.31140, .050$	$r_{71,45} = -0.29640, .051$	
Heading date	4	$r_{74} = -.2212, .053$	$r_{74,15} = -.3072, .050$	
Ripening date	5	$r_{75} = +.2202, .052$	$r_{75,14} = +.3342, .049$	$R_{5,145} = 0.56020, .054$
Test weight and F_5 rust	1	$r_{71} = -.4552, .054$	$r_{71,45} = -.4502, .051$	
Heading date	4	$r_{74} = -.2092, .057$	$r_{74,15} = -.7162, .059$	
Ripening date	5	$r_{75} = +.2292, .075$	$r_{75,14} = +.4902, .051$	$R_{5,145} = 0.74220, .057$
Gasoline color and Test weight	6	$r_{73} = -.5582, .055$	$r_{73,45} = -.5542, .059$	
Ripening date	5	$r_{75} = -.2092, .051$	$r_{75,45} = -.1212, .078$	$R_{5,45} = .5572, .054$
Crude protein content and	7			
F_5 rust	1	$r_{71} = -.2642, .049$	$r_{71,45} = -.4592, .044$	
Heading date	4	$r_{74} = +.2282, .052$	$r_{74,15} = +.4552, .045$	
Ripening	5	$r_{75} = -.2672, .048$	$r_{75,14} = -.4102, .046$	$R_{7,145} = .5692, .050$

As shown by the partial correlations, rust and dates of heading and ripening had about equal influence on yield. None of these correlations was very high. It is significant, however, that the partial correlation coefficients for yield with heading and ripening dates were higher than those for simple correlation. This indicates that the correlation between heading and ripening together with their conflicting effect on yield masked their respective true relations with yield.

The conflicting effects of heading and ripening dates are again brought out in relation to test weight. The partial correlation coefficients for test weight with rust and heading and ripening dates are all higher than were the simple correlations. From a comparison of the partial correlations, it appears that heading date had the most effect on test weight. However, since test weights were only available on the 72 higher yielding strains, it may be that test weights on the remaining 78 strains would have indicated that rust had more effect on the variability of test weight than did heading.

The data also indicate that test weight had much more influence on gasoline color than did date of ripening.

Again in the case of per cent crude protein, the masking effect of the correlation between heading and ripening

dates is demonstrated. The partial correlations of both heading and ripening dates with per cent protein are higher than the corresponding simple correlations. The correlation between rust and protein is also accentuated, though not in so great proportion.

Multiple correlations. By the use of multiple correlations it is possible to show how much of the total variability of a given character is caused by the other characters under study. From the multiple correlation values it is seen that only about 30 per cent of the total squared variability (variance) of yield in F_3 is caused by rust, date of heading, and date of ripening. In the case of test weight about 54 per cent of the total squared variability is caused by the three characters studied. It was also found that 32 per cent of the total squared variability of gasoline color is caused by test weight and date of ripening. For protein about 35 per cent of the variance was caused by rust, and heading and ripening dates. Factors other than the ones here considered evidently have considerable influence on the characters yield, test weight, gasoline color value, and crude protein content.

A comparison of the coefficients of multiple correlation shows that a larger proportion of the variability has been accounted for in test weight than in yield. This again sug-

gests that yield is the result of a more complex set of factors than is test weight.

Characters not correlated

No important or significant correlations were found between rust infection and dates of heading or ripening and gasoline color value. The average yield of F_3 strains was not correlated with the yield of the F_2 parent plants, with the per cent of crude protein, nor with their gasoline color value. Test weight was not correlated with protein. There also was no correlation between date of heading nor per cent of crude protein and gasoline color value.

Relations of Kernel Color to other Characters

Results were obtained on the relation of color of kernel to the other characters studied. These data are shown in Table XIV. The relations generally are not statistically significant, but their consistency may indicate that they are caused by something more than chance variation.

The red kernelled strains were slightly but not significantly more rusty in both the F_2 and in the F_3 than the amber strains. In the F_3 the strains segregating for color were intermediate in rust reaction between the homozygous red and amber strains. The parents, however, react to rust in the opposite manner, i. e., Pentad (red kernels) is much

more rust resistant than Akrona (amber kernels)

In the F_2 generation the average yield of the amber strains was higher than that of the red strains. The difference, however, was not significant in the light of the probable errors. There appears, however, to be a consistent relation between kernel color and yield, because in 1930, the average yield for the strains with amber kernels was lower than that of the red strains, their order being the same as that of the parents. The segregating strains were intermediate in average yield between the red and amber strains.

In 1930 the Pentad parent was consistently higher in test weight than Akrona. The mean test weights of the red and amber F_3 strains show significant differences in the same order as the parents. The amber F_3 strains have a lighter test weight than the red strains in spite of the fact that they were not more rusty.

Table XIV.—The relation of kernel color to other characters in the Pentad x Axtron durum wheat cross and in the parents at Langdon, N. Dak., in 1926 and 1930

Characters	Kernel color		
	Red	Segregating	Amber
F_1 rust infection Hybrids (per cent)	33.5 ± 0.9		31.5 ± 0.9
Parents "	6.2		80.9
F_2 rust infection Hybrids (per cent)	35.3 ± 1.0	31.7 ± 1.0	31.4 ± .9
Parents "	6.6 ± .6		48.7 ± .6
F_2 yield Hybrids (gms./plot)	5.66 ± .17		6.97 ± .23
Parents "	5.61		6.98
F_3 yield Hybrids "	3.83 ± .14	3.71 ± .08	3.87 ± .06
Parents "	4.26 ± .16		2.62 ± .16
Test weight (Lbs./bu.)			
Hybrids	59.8 ± .1	59.3 ± .1	59.1 ± .1
Parents "	59.1 ± .01		58.9
Heading date (July*)			
Hybrids	18.1 ± .2	16.8 ± .1	16.9 ± .1
Parents "	16.9 ± .1		16.4 ± .2
Blooming date (August*)			
Hybrids	21.1 ± .3	20.7 ± .1	20.0 ± .1
Parents "	21.4 ± .2		19.6 ± .1
Glutelin color value			
Hybrids	1.16 ± .07	1.20 ± .012	1.22 ± .013
Parents "	.76 ± .05		1.07 ± .015
Glut protein content			
1926 parents			
F_1 hybrids	16.2		16.1
1930 parents	14.5 ± .12	14.1 ± .06	14.0 ± .05
	14.9 ± .06		13.6 ± .04

The relation between heading date and kernel color is not definite. Possibly the data might be interpreted to indicate a tendency for the red F_3 strains to be slightly later in heading than the amber strains.

The relation between kernel color and date of ripening appears more definite. Here the red F_3 strains are one day later in ripening than the amber strains, while the strains segregating for color are intermediate. These differences are not very great but probably are significant in view of the fact that the two-day difference between the parents has been repeatedly observed. If such a relation holds, we should expect the red-kernelled strains, which ripen later than the amber strains, to carry a higher yield and a higher test weight than the amber strains. This was the case.

Significant differences were obtained between the gasoline color values for the red and amber kernel color groups. These differences corresponded to the differences observed in the parents. The red-kernelled F_3 strains had a mean gasoline color value of $1.16 \pm .07$, the segregating kernel color group $1.20 \pm .02$, and the amber kernel colored group $1.32 \pm .03$. If this relation holds true in other crosses it will be of much value in selecting strains for desirable quality, and suggests that from the standpoint of quality there will be valid objection to continuing red-kernelled strains. There was a definite but not statistically significant tendency for the

red strains to be higher in protein content than the segregating or amber kernelled strains.

SUMMARY

The F_2 and F_3 generations of the Pentad x Akrona durum wheat cross were studied for segregation of and associations among the characters, stem rust, kernel color, yield, test weight, heading date, ripening date, gasoline color value, and crude protein content. In the F_2 , 184 plants and in the F_3 , 150 strains were grown.

The parent and hybrid material was classified for stem rust infection on an individual plant basis. The results showed that rust reaction was inherited as a quantitative character. In the F_2 the distribution of the hybrid plants was intermediate between the parents and resembled a normal curve, with 30 per cent rust as the modal class. The average rust percentage was 31.7. By correcting the F_2 distribution from the F_3 strains grown there was indication of partial dominance of susceptibility. Very few of the plants or strains had the resistance of Pentad while many of them were as susceptible as Akrona. The high correlation between the F_2 and the F_3 stem-rust infections indicated that the epidemic was caused by the same physiologic form or group of forms in the two seasons, and that the results obtained were a true measure of the inherent reactions of the

F_2 plants to rust. The F_3 plants showed evidence of continuance of segregation for homozygous types in the recovery of the stronger resistance of Pentad. Classification of the F_3 strains for homozygosity on the basis of the standard deviation in line with that of the parents indicated that 22 per cent of the F_3 strains were homozygous. This percentage of homozygosity would be expected of the F_3 strains if five factors of equal effect were responsible for the rust reaction. Two or three major and other minor factors may control the reaction to stem rust in this cross.

The data for kernel color did not fit any Mendelian ratio satisfactorily. A fair fit was obtained to a ratio of 9 red to 7 amber kernels in the F_2 generation and to a 1:8:7 ratio for red, segregating, and amber in the F_3 . This might be explained on the basis of two complementary factors for red kernel color. Thus Pentad would have the genotypic constitution AAbb, Akrona, nabb. It is pointed out that if this hypothesis is correct it should be possible to cross two amber kernelled plants, AAbb with aabb, and obtain a red-kernelled F_1 , AaBb.

The average yield per plant of the hybrids was intermediate between the average yields of the parents, in both generations. In both seasons the average yields of the parents were significantly different. In 1939, Akrona, and in 1930 Pentad made the higher yield. The reversal of rank of the

parents as to yield in the two years is attributed to the fact that the rust caused more damage to the crop in 1930 than in 1929.

Data on test, weight, date of heading, date of ripening, gasoline color value and crude protein content were obtained in the F₃ generation, on each F₃ strain and parent check row. The average of the hybrids for each character was intermediate between the averages of the parents. Transgressive segregation was indicated in test weight per bushel, date of heading, and date of ripening. Low gasoline color value appeared to be partially dominant over high color.

Associations between characters were studied by means of averages, and simple, partial, and multiple correlation coefficients.

In 1930 when rust caused obvious damage significant negative correlations were obtained, for rust infection with yield, test weight, and protein content. The negative correlation between rust and test weight was larger than that for rust and yield, indicating that test weight is more directly affected by rust than is yield. A positive correlation between rust and heading date showed only a slight tendency for the early heading strains to avoid severe rust infection. Thus the rust epidemic was severe enough to injure the susceptible plants regardless of date of heading. No correlation was obtained for rust and ripening date or rust

and gasoline color value.

No correlation was found between yield in F_2 and F_3 . The F_3 strains with higher yield tended to have higher test weights and earlier heading and later ripening dates than the lower yielding strains. No correlation was found for yield with gasoline color value nor protein content. The effects of rust and heading and ripening dates on yield were studied by means of partial correlation coefficients. These revealed a decreased relation between rust and yield and emphasized the relations of heading and ripening to yield. The multiple coefficient of correlation of rust, heading, and ripening dates with yield indicated that about 30 per cent of the squared variability or variance in yield had been accounted for by the factors under observation.

Simple correlation coefficients showed that strains high in test weight tended to be earlier in heading, later in ripening, and lower in gasoline color value than strains lower in test weight. These relations were emphasized by a comparison of the averages of the characters for strains on which test weights were taken, with the averages for the strains on which test weights were not available because of insufficient grain.

Partial correlation coefficients for rust, heading, and ripening dates with test weight accentuated the relations, particularly the correlation between test weight and heading.

A multiple correlation coefficient showed that more of the squared variability or variance in test weight had been accounted for than in yield, about 54 per cent being caused by rust, and heading and ripening dates.

Heading date showed small but significant positive correlations with ripening date and protein content but no correlation was found between heading date and gasoline color value.

There was some tendency for strains with early dates of ripening to be higher in gasoline color value than the later strains. When the effect of test weight was eliminated by the use of partial correlation, the tendency was not so marked. Partial coefficients of correlation of test weight and ripening date with gasoline color value tended to reduce the relations between these characters and gasoline color value. The multiple correlation coefficient indicated that 38 per cent of the squared variability or variance in gasoline color value had been accounted for.

A small negative correlation was obtained between ripening date and protein content. The small negative correlation between gasoline color and protein was hardly significant. Partial correlations accentuated the relations of rust reaction, and heading and ripening dates to protein and the multiple correlation for protein content when these characters were considered showed that about 35 per cent of the

variance in protein was caused by these three characters.

A study of the relation between kernel colors and the other characters revealed some significant differences. The Akrona parent is earlier than Pentad. The amber strains of the cross were earlier than the red strains, while the segregating strains were intermediate. The positive correlations of yield and test weight with date of ripening may in part be responsible for the tendency for red strains to be higher both in yield and test weight than the amber strains. The red-kernelled strains showed a significantly lower gasoline color value than the amber-kernelled strains. This information should prove useful in selection of durum wheat for quality.

The study indicates that from both the commercial and the agronomic point of view, the desired durum variety should be rust resistant, amber kernelled, high in gasoline color value, moderate in protein content, early in heading and late in ripening with consequent high yield and test weight.

ACKNOWLEDGMENTS

The writer wishes to express appreciation to Dr. John H. Parker, Professor of Crop Improvement, Kansas State Agricultural College, who served as major instructor; to Mr. J. Allen Clark, Senior Agronomist, U. S. Department of Agriculture, for advice in outlining the experiment, for furnishing the material, for assistance in gathering the data, and for editing the manuscript; to Drs. K. S. Quisenberry, Associate Agronomist, U. S. Department of Agriculture, and L. R. Waldron, Plant Breeder, North Dakota Agricultural Experiment Station, for suggestions in gathering the data and editing the manuscript, to Doria Smith for help in assembling the data; and to all others who have contributed to the completion of this thesis.

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